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Misperceiving space following shifts of attention: Determining the locus of the attentional repulsion effect

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ABSTRACT

The Attentional Repulsion Effect (ARE) is a spatial consequence of allocating attention to peripheral locations. Specifically, a shift in attention to the periphery produces an error in the localization of visual objects in the opposite direction of the shift. Suzuki and Cavanagh proposed three possible mechanisms to account for the neural basis of the repulsion effect; surround suppression, RF shrinking, and RF recruitment. The purpose of the present experiment was to begin to investigate the ARE mechanism by determining its locus. This was achieved by assessing both monocular and binocular vision, and then by examining AREs in a condition that assesses interocular transfer, where the cue is only presented to one eye and the target is only presented to the other eye. Importantly, this latter test allowed for a direct verification of the ARE's locus. Given that the magnitude of the repulsion effect was nearly identical in the two vision conditions, and that the effect disappeared in the interocular condition, the current findings indicate that the ARE occurs early in visual processing, prior to or in the input layers of V1 and before binocular vision dominates.

1. Introduction

When a sensory event occurs in the periphery of the visual field, such as the abrupt appearance of anew object, the focus of our attention tends to be reflexively oriented to the location of the event. The temporal consequences of this reflexive orienting have been extensively researched and are very well known: target objects that subsequently appear at the location of the initial event (termed a cue) are detected more quickly than targets that appear at locations other than the cued location. This attention cueing effect typically occurs if the delay between the cue and the target is less than 200 ms (Posner, 1980; Theeuwes, 1991). Although there is considerable evidence regarding the effects of transient attention on accuracy in detection and discrimination tasks, contrast sensitivity, visual search performance, and spatial resolution (see Carrasco, 2011, for a review; see also Carrasco, Fuller, & Ling, 2008; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Ling & Carrasco, 2007; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2008), the effects of attention on the perception of spatial locations have been rarely investigated and as such are more poorly understood.

Prompted by the results of physiological studies suggesting that attention can modulate the spatial properties of individual receptive fields in V4 (Connor, Gallant, & Van Essen, 1994), the inferior temporal lobe (IT) (Rolls, Aggelopoulos, & Zheng, 2003), the medial temporal area (MT) (Anton-Erxleben, Stephan, & Treue, 2009; Womelsdorf et al., 2006), and the lateral intraparietal area (LIP) (Ben Hamed et al., 2002). Suzuki and Cavanagh (1997) sought to determine whether measurable spatial effects could be elicited by the reflexive shifts of attention made to peripheral cues. Interestingly, they discovered that these shifts of attention could alter the spatial perception of target stimuli presented at a central location. The basic paradigm they employed required observers to fixate on a cross at the center of a screen while a brief peripheral circular cue appeared in either of the upper two quadrants of the display. Subsequently, a brief Vernier stimulus was presented along the vertical meridian and was followed by the appearance of a random dot mask. In a two-alternative forced choice task, observers indicated whether the Vernier was off-set clockwise or counterclockwise by pressing keys on a computer keyboard. Interestingly, when the cue was in the top left quadrant, participants reported an offset in the clockwise direction and when the cue appeared in the top right quadrant, participants reported and offset in the counter clockwise direction. In other words, the Vernier was most often perceived to be displaced in the opposite direction from where the peripheral cue captured attention. Suzuki and Cavanagh coined this effect the attention repulsion effect (ARE).

Following up Suzuki and Cavanagh's original report on the ARE, Pratt and Turk-Browne (2003), and Pratt and Arnott (2008), confirmed that a shift in attention to the periphery produces an error in the localization of visual objects in the opposite direction of the

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shift. For example, Pratt and Arnott (2008) provided evidence for the ARE being attentional in nature by assessing Vernier line judgments in three different cue settings: onset vs. offset cues, simultaneous appearance of onset and offset cues in different locations, and pop-out cues. The effects on reaction times in each of these three scenarios are well-known (Godijn & Theewues, 2004; Pratt & Hirshorn, 2003; Pratt & McAuliffe, 2001; Rauschenberger, 2003). In all three cases, the known pattern of RT cueing effects were reproduced in spatial repulsion effects, suggesting that it is attention that underlies the ARE. Furthermore, these results show that the ARE can be modulated reliably and that it is sensitive to cue changes, prompting Pratt and Arnott to propose that the ARE may be more sensitive than a temporal gauge of distribution of attention because spatial measures may have less variability than RTs. In other words, the ARE may be a very sensitive and useful tool for quantifying the capture of attention. There is also evidence that receptive field shifts towards the focus of transient attention could account for stimuli there being judged to be bigger than stimuli at uncued locations (Anton-Erxleben, Henrich, & Treue, 2007). Indeed, the same mechanism could explain the effect of transient attention on perceived object shape found by Fortenbaugh, Prinzmetal, and Robertson (2011).

To account for why the ARE occurs, Suzuki and Cavanagh (1997) suggest that the repulsion effect represents the cost of orienting attention in order to enhance perception at a peripheral location, a hypothesis that is based on several assumptions. The first one is that spatial locations are represented by a population of 'position-coding' neural units that have spatially localized receptive fields. Suzuki and Cavanagh also state that these neural units could be composed of cells from any visual area that preserves retinotopy. Further, they put forth that the target display (Vernier) will be coded in terms of the centroid of these position-coding neural units. Presumably, without peripheral cues the population centroid representing the perceived Vernier location would correspond to the veridical location. Conversely, the appearance of a peripheral cue would shift the focus of attention to the cued location, adjusting the centroid of the distribution such that the Vernier appears displaced away from the focus of attention (i.e., the cued location). Thus, Suzuki and Cavanagh suggest that the ARE occurs because the position of the centroid of the response distribution of receptive fields will be skewed away from the focus of attention.

How could a modulation of the distribution of reception fields generate an ARE? Suzuki and Cavanagh (1997) propose three possible mechanisms. One mechanism is surround suppression, where the cell activity surrounding the focus of attention could potentially be suppressed by lateral inhibition, resulting in the attended location receiving greater spatial selectivity due to inhibition of interference from neighboring cells. Another mechanism is receptive field (RF) recruitment, whereby RF's near the attended location presumably shift towards it and as a result, respond less than usual to stimuli in the area bordering the focus of attention. The final mechanism is RF shrinking, where RF position tunings sharpen (i.e., shrink) around the focus of attention and, similar to the recruitment mechanism, these shrunken RF's respond less than they normally would to stimuli surrounding the focus of attention, resulting in the population response being skewed away from the attended location.

Although Suzuki and Cavanagh (1997) provided three possible mechanisms for the ARE, they were agnostic as to which one might ultimately provide the most viable account. To date, the ARE mechanism has yet to be elucidated. The purpose of the present experiment is to take a first step towards uncovering this mechanism by determining the locus of the ARE, which will eventually be accomplished by assessing the relative contributions of monocular and binocular processes. Receptive fields in the visual system are organized hierarchically, such that activation of RF's in ganglion cells of the retina require less complex stimuli than RF's in the primary visual cortex (V1) or in the inferior temporal lobe (IT). It has long been recognized that the lateral geniculate nucleus (LGN) represents the first stage in the visual system where it is possible for RF's to receive binocular input. Yet according to Hubel and Wiesel (1962), binocular cells in the LGN likely constitute, at best, a small minority of the total cells, meaning that the vast majority of input to the LGN is monocular. Similarly, in primary visual (striate) cortex there exist numerous monocular neurons comprised of RF's similar in constitution to those residing in the LGN (van der Zwan et al., 1998), It is important to note, however, that V1 also marks the earliest stage in the visual system that contributes to the generation of binocular vision. Although its full complexity can only be accounted for by regions in the extrastriate cortex, neurons in V1 perform some initial binocular spatiotemporal filtering. Nonetheless, it stands to reason that if the ARE required binocular vision, its neural correlates would likely reside in the higher order visual processing areas of the extrastriate cortex – V2–V5 – because the neurons in these areas are more closely involved in controlling stereoscopic vision than neurons in V1 (Dodd et al., 1996).

When Hubel and Wiesel (1959, 1962) began the laborious process of mapping out physiological recordings from receptive fields in various parts of the visual system, they noted the corresponding retinal regions of binocular neurons worked in synergy. That is to say that simultaneous stimulation of equivalent RF's elicited a response that was unmistakably stronger than the response from one of the RF's on its own. Activation of both of the retinal RF's in a binocular neuron had a summative effect in the striate cortex. From this, Hubel and Wiesel hypothesized that any binocularly activated unit which could be affected by stimulation from one eye alone should be much more strongly influenced when both eyes are used. Indeed, studies comparing the performance of monocular and binocular vision in various behavioral attentional settings reveal binocular superiority as measured by reaction time or accuracy. For example, Jones and Lee (1981) demonstrate that regardless of stereopsis or eye dominance, the use of both eyes results in significantly faster RT's when subjects were asked to recognize subtle differences in hue and to detect camouflaged octopi in a visual scene. Similarly, Sheedy et al. (1986) report that subjects restricted to monocular vision generate slower RT's when identifying lines from an eye chart and when picking out the number of 'R''s in a sentence. Such findings are not restricted to human observers, as Stefano, Kusmic, and Musumeci (1987) also found that pigeons are better able to discriminate between horizontal and vertical gratings while utilizing binocular vision as opposed to monocular. Additionally, Stefano, Kusmic, and Musumeci (1987) suggest that summation alone likely accounts for the differential in RT's between conditions, a notion that lies in agreement with Hubel and Wiesel's (1959, 1962) initial findings.

The present experiment is based on three findings from the literature. The first finding, as noted by Suzuki and Cavanagh (1997), is that attention can modulate RFs. Indeed, numerous physiological studies have shown that voluntary attention can modulate the response of cells to preferred stimuli (e.g., Bushnell, Goldberg, & Robinson, 1981; Mountcastle et al., 1987; Spitzer & Richmond, 1991), and some have even shown that attention can modulate the spatial properties of individual RF's (Anton-Erxleben, Stephan, & Treue, 2009; Ben Hamed et al., 2002; Connor, Gallant, preddie & Van Essen, 1996; Connor, Gallant, & Van Essen, 1994; Connor, preddie, Gallant, & Van Essen, 1997; Desimone et al., 1990; Moran & Desimone, 1985; Womelsdorf et al., 2006). The second finding is that in the aforementioned attentional tasks, the activation of binocular RFs yields better accuracy and faster RTs as compared to when only monocular RFs are activated (Hubel & Wiesel, 1959, 1962; Jones & Lee, 1981; Sheedy et al., 1986; Stefano, Kusmic, & Musumeci, 1987). The third finding is that although some binocular RFs do ex-

ist in V1, binocular processing largely occurs in areas V2, V3, V4 or V5 as these are the regions that ultimately control stereoscopic vision (Dodd et al., 1996; Gazzaniga, 1999; Hubel & Wiesel, 1962).

Given these three findings, it is possible to make predictions about the locus of the ARE. The following three experiments reveal information about where the ARE originates within the visual stream. Experiment 1 tests whether the ARE will emerge under monocular conditions. Experiment 2 confirms that the ARE is truly a monocular process, as an interocular condition (where the cue was presented to one eye and the target to the other eye) did not yield an ARE. Results from Experiment 3 ensure that the lack of an interocular ARE was not due to transient visual signals.

2. Experiment 1

The current experiment uses a paradigm identical to the one used by Pratt and Turk-Browne (2003) to find the attentional repulsion effect, which in turn was based on Suzuki and Cavanagh's (1997) initial study. Two simultaneous brief peripheral cues (either top left + bottom right or top right + bottom left) were presented before a short-lived Vernier stimulus, which was subsequently masked. In the present experiment, the bottom Vernier was always aligned with the central fixation point, whereas the top Vernier line could appear at one of three locations (left, center, right). Subjects were required to make a forced-choice decision as to whether the top line appeared to the left or right of the bottom line. An ARE is expected to be found; top-left + bottom-right cues biasing the perception of the top line to the right of the bottom line and top-right + bottom-left cues biasing the perception of the top line to the left of the bottom line. Importantly, the task is performed both binocularly and monocularly.

It follows then, that there are three plausible outcomes for the current experiment: first, the monocular condition might fail to reveal an ARE; second, the strength of the monocular ARE may be significantly smaller than the binocular ARE; finally, the two conditions may yield AREs of identical magnitude. If an ARE is not detected in the monocular condition, it would necessarily require the involvement of a post-V1 based mechanism. In the second scenario, where the monocular condition yields a significantly smaller ARE compared to the binocular condition, it would seem likely that a mixture of pre and post-V1 based mechanisms would be involved, and a definitive locus would be difficult to pinpoint. In the final scenario, where the monocular and binocular conditions yield AREs of identical strength, having use of both eyes as opposed to one does not provide additional resources that give rise to a stronger ARE. Theoretically, then, it is tempting to suggest that the ARE may be governed solely by a mechanism that originates prior to the converging of information from the left and right visual world. There is, however, the possibility that monocular input could activate binocularly-tuned cells in a magnitude identical to input from binocular receptive fields.

2.1. Methods

2.1.1. Subjects

Fourteen undergraduate students from the University of Toronto participated in the experiment in partial fulfillment of their Introductory Psychology course credit. All participants had normal or corrected-to-normal vision and were naive as to the purpose of the task, which lasted 45 min. Additionally, all subjects gave their informed consent prior to participation and were subsequently debriefed.

2.1.2. Apparatus and methods

The experiment was conducted on a PC computer with a VGA monitor, and a head/chin rest was used to ensure a viewing distance of 44 cm. Attached to the head/chin rest was an adjustable eye occluder which was used in the monocular condition to occlude vision in the subjects' dominant eye. Each subject was tested individually in a dark, sound attenuated room.

All stimuli appeared in white (30.0 cd/m^2) on a black (0 cd/m^2) background, and the basic trial sequence appears in Fig. 1. The initial screen displayed a central fixation cross (.25° in diameter) that remained for 1000 ms. Then, two cues consisting of filled circles, 1.44° in diameter, appeared for 50 ms in either the top-left and bottom-left areas of the display or the top-right and bottom-left areas of the display. The centers of the circles were displaced 6.3° in the horizontal and vertical directions from the central fixation cross. Following the removal of the cues, there was a delay of 50 ms during which the central fixation cross remained displayed. At this point the fixation cross was removed and the Vernier target appeared, consisting of two vertically aligned lines. Each line was 1.44° long and 0.1° wide and the midpoint of each line was displaced 5.6° in the vertical direction away from the center of the screen. While the bottom line always appeared directly below the location that the fixation cross had previously occupied, the top Vernier line could appear in one of three location; directly above the bottom line (0° position), to the left of the bottom line (−0.36° position), or to the right of the bottom line (+0.36° positions). In terms of pixels from the center location, the three possible target locations were −9, 0, +9 pixels for the left, center, and right target locations, respectively. The Vernier target was

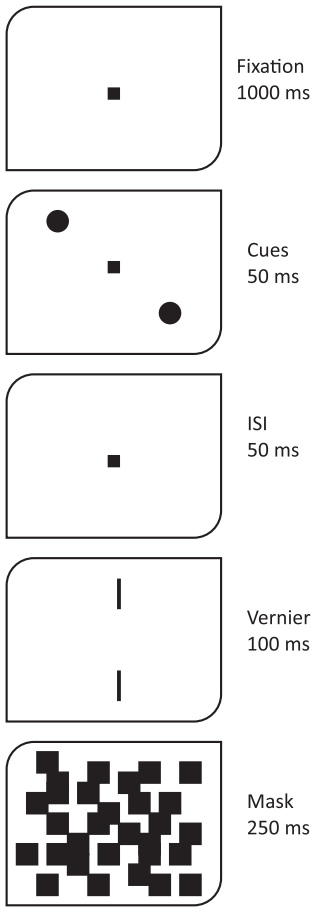

Fig. 1. The basic trial sequence used in the experiment. In the actual experiment, the background was black and the stimuli were white.

displayed for 100 ms and then removed and replaced by a pattern mask (consisting of 150 randomly positioned squares each subtending 0.25°) that was presented for 200 ms. Participants were instructed to remain fixated at the center of the screen throughout each trial and to determine whether the top line was to the left or right of the bottom Vernier line. If they perceived the top line was to the left, they were to press the 'z' key with their left index finger and if they perceived the top line was to the right, they were to press the "/" key with their right index finger. After each response, there was a 1000 ms intertrial interval before the fixation cross reappeared to begin the next trial. If the subject pressed a key other than "z" or "/" or if the subject did not press a key within a 2000 ms timeframe, an error beep sounded and the program continued to the next trial.

A within-subject design where each participant completed 180 trials in each of the two blocked conditions (monocular, binocular) was used. Throughout each session, it was equally likely that the cues would be the top-left + bottom-right combination or the top-right + bottom-left combination. The three positions of the upper Vernier target line were also randomized across the session as was the order of condition.

2.2. Results and discussion

The percentage of "left" responses (the percentage of times the top Vernier line was perceived as being to the left of the bottom Vernier line) was calculated for each of the three top-line positions. The mean left responses appear in Fig. 2 and were analyzed using a 2 (condition: monocular or binocular) × 2 (cue: top-left + bottom-right or top-right + bottom-left) × 3 (top Vernier line position: −9, 0, 9) analysis of variance (ANOVA). A main effect was found for target position ($F(2,26) = 37.0$, $p < 0.00001$), as the percentage of "left" response decreased as the top Vernier line moved from the leftmost target to the rightmost target (71.1% at −9, 50.7 at 0, and 25.7 at +9). This demonstrates that participants were able to distinguish between the three target locations regardless of which cue was present or which condition was being tested. A main effect for cue was also found ($F(1,13) = 7.8$, $p = 0.01$), with top-left and bottom-right cues resulting in fewer "left" responses (39.0%) than top-right and bottom-left cues (59.5%). This indicates that an ARE was present, as subjects were more likely to perceive the top line in the opposite direction of the cue. No main effect was found for condition, nor did viewing condition interact with any other variable, ($F(1,13) < 1$), indicating that there were no statistical differences in responding. The cue by Vernier position interaction was the only interaction that reached significance, $F(2,26) = 3.58$, $p < 0.05$, with the ARE being greatest at the 0° target position and decreasing in magnitude in both the left and right target positions.

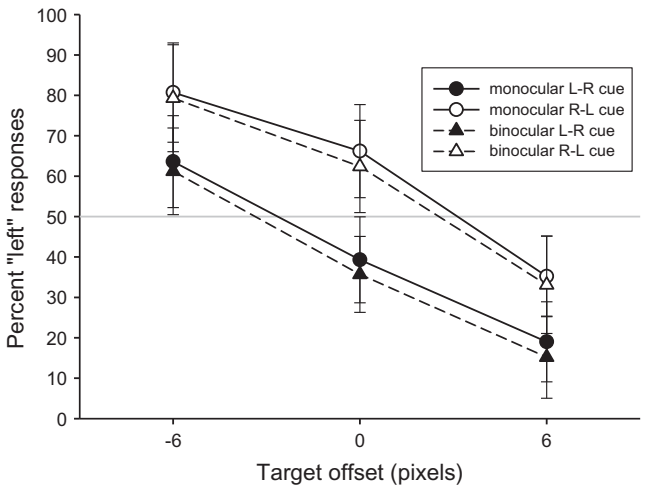

Fig. 2. The mean percentage of "left" responses for the monocular and binocular conditions in Experiment 1. The cues were either top left–bottom right (L–R) or top right–bottom left (R–L). Error bars represent standard error.

The strongest test of the ARE comes from an analysis of the 0° target condition, as here we can see any perceived misalignment when in reality the two parts of the Vernier target are aligned. For this analysis we used a 2 (condition: monocular or binocular) × 2 (cue: top-left + bottom-right or top-right + bottom-left) ANOVA on only the 0° condition. Similar to the previous analysis, there was an effect of cue, $F(1,13) = 10.76$, $p < 0.01$), no effect of condition, $F(1,13) < 1$, and no interaction between cue type and condition, $F(1,13) < 1$. These results are consistent with the third possibility presented at the start of this experiment; the locus of the ARE occurs very early in visual processing before the input from the left and right visual fields are combined. To verify this conclusion, however, an additional experiment is necessary.

3. Experiment 2

The preceding experiment revealed two critical pieces of information: first, that the ARE is indeed observed monocularly; second, that it is of the same magnitude an ARE generated during binocular tasks. Although these results suggest the likely involvement of a mechanism that originates in early visual processing areas, there is still the possibility that the ARE could arise in high-level areas with binocular tuning, or that monocular input could be sent to high-level areas and activate binocular-tuned cells Hubel and Wiesel (1959, 1962). Therefore, the purpose of the current experiment is to pinpoint the locus of the ARE. Is it prior to V1 – before binocular vision dominates, or is it post-V1 – where receptive fields are fully attuned to the blending of information from the left and right visual fields and where neurons account for the full complexity of stereoscopic vision?

To address this essential question, we employed the use of visual occlusion spectacles allowing us to create a condition assessing interocular transfer, where the cue was seen by one eye only and the target was only seen by the other eye. If a repulsion effect is observed under these circumstances, it will necessarily implicate binocular processes. The reason for this is that an ARE requires the onset of a peripheral cue as well as detection of a target location: in the interocular condition, the eye that is responsible for determining the location of the target will not have seen the cue. Therefore, if an ARE is observed, there would unavoidably have been crosstalk between the two eyes. The task is forced-choice, and thus the expectation without binocular interaction would be that subjects would report a 'left' target approximately the same percentage of the time that they report a 'right' target.

Here we compare a monocular condition, where an ARE is expected, with an interocular condition, where the expectation is that no ARE will be found.

3.1. Methods

3.1.1. Subjects

Twenty-six undergraduate students from the University of Toronto participated in the experiment in partial fulfillment of their Introductory Psychology course credit. All participants had normal or corrected-to-normal vision and were naive as to the purpose of the task. Additionally, all subjects gave their informed consent prior to participation and were subsequently debriefed.

3.1.2. Apparatus and methods

This experiment used same apparatus and method as the first experiment, except that PLATO (Portable Liquid–Crystal Apparatus for Tachistoscopic Occlusion) Visual Occlusion goggles were worn during the task. This device allows for controlling the timing of presentation of visual information during an experimental task. The spectacles were controlled by connecting them to the PC system using a parallel port, and ToTaLcontrol software provided two independently driven signals, one for each lens.

Using the LCD goggles, two groups of subjects performed different conditions. For these conditions, both lenses were transparent at the start of each trial and when a response was recorded to end each trial. One group of subjects replicated the monocular condition of the first experiment, although now vision to one eye was blocked by having one of the lenses of the LCD goggles turn opaque when the fixation point appeared and remained so until a response was made. The other group of subjects performed the interocular condition. This condition used the same timing as the monocular condition, but here one lens would be opaque during the cue presentation while the other lens would be opaque during the target presentation. Thus, one eye would only see the cue and the other eye would only see the target. In this between-subjects design each subject completed 180 trials.

3.2. Results and discussion

The percentage of left responses was calculated for each of the three target positions. The mean left responses appear in Fig. 3 and were analyzed using a 2 (condition: monocular or interocular) × 2 (cue: top-left + bottom-right or top-right + bottom-left) × 3 (top circle position: −9, 0, 9 pixels) ANOVA. A main effect was found for target position, $F(2,48) = 191.8$, $p < 0.0001$, as the percentage of "left" responses decreased as the top target moved from the leftmost location to the rightmost location (82.7% at −9, 51.6% at 0, and 14.9% at +9). This demonstrates that participants were able to distinguish between the three target locations regardless of which cue was present or which condition was being tested. There was no main effect for cue, $F(1,24) < 1$, indicating that top-right and bottom-left cues resulted in similar numbers of left responses as top-left and bottom-right cues (49.8% and 53.3%, respectively). There was also no main effect for condition, $F(1,24) < 1$. The cue by condition interaction reached significance ($F(1,24) = 5.9$, $p < 0.05$), with top-left cues and bottom-right cues eliciting less 'left' responses than top-right and bottom-left cues in the monocular condition but not in the interocular condition, meaning that presence of opposite cue types elicited an ARE in the monocular condition but had no effect in the interocular condition. The cue by target interaction did not reach significance ($F(2,48) = 3.6$, $p > 0.05$) because although the ARE effect was greatest at the 0 pixel position and lessened at both the −9 and 9 positions in the location condition, this effect was not present in the interocular condition, implying that there was no repulsion effect present when subjects viewed the cue with only one eye and the target with only the opposite eye.

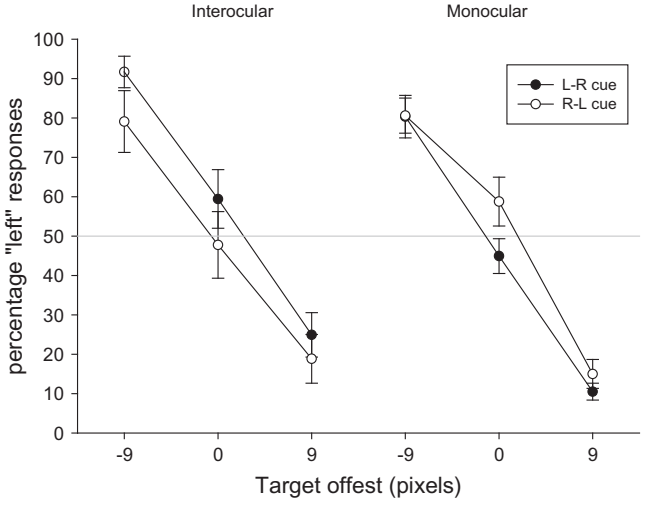

Fig. 3. The mean percentage of 'left' responses for the monocular and interocular conditions in Experiment 2. The cues were either top left–bottom right (L–R) or top right–bottom left (R–L). Error bars represent standard error.

In order to specifically analyze results from the 0° position, which is where participants consistently perceived misalignment when in reality the Vernier targets were aligned, a 2 (condition: monocular vs. interocular) × 2 (cue: top-left + bottom right or top-right + bottom-left) ANOVA was used. Once again, there was an interaction between cue and condition ($F(1,24) = 4.44$, $p < 0.05$), demonstrating that alternating cue types had different effect in each condition – for the monocular condition, it resulted in an ARE, whereas for the interocular condition, it did not. These effects were confirmed by paired *t*-tests, which showed a significant difference in cueing for the monocular condition ($t(11) = -2.85$, $p < 0.05$) but not the interocular condition ($t(11) = 1.02$, $p > 0.05$). These findings strongly suggest that the ARE occurs early in visual processing before information is combined across the eyes.

4. Experiment 3

The previous experiment involved extremely rapid opening and closing of eye-shutters. It is therefore possible that the lack of ARE in the interocular condition is due to interference from transient visual signals and not to a monocularly driven mechanism. In order to rule out this possibility, a visual transient was introduced into the monocular condition whereby the shutters were opened and closed during the time between the onset of cue and target. If indeed the transient was interfering with the ARE, we should see a disappearance of the repulsion effect in the monocular condition.

4.1. Methods

4.1.1. Subjects

Six undergraduate students from the University of Toronto participated in the experiment in partial fulfillment of their Introductory Psychology course credit. All participants had normal or corrected-to-normal vision and were naive as to the purpose of the task. Additionally, all subjects gave their informed consent prior to participation and were subsequently debriefed.

4.1.2. Apparatus and methods

The experiment consisted of two blocked conditions; the monocular condition from Experiment 2 and a transient condition. The transient condition was exactly the same as the monocular condition except that after the offset of the cue, the open lens was shut for 4 ms (the shutter speed of the goggles) and then reopened. This produced a similar visual transient as that seen in the interocular condition of Experiment 2.

4.2. Results and discussion

The percentage of left responses was calculated for each of the three target positions; they appear in Fig. 4 and were analyzed using a 2 (condition: monocular or transient) × 2 (cue: top-left + bottom-right or top-right + bottom-left) × 3 (top circle posi-

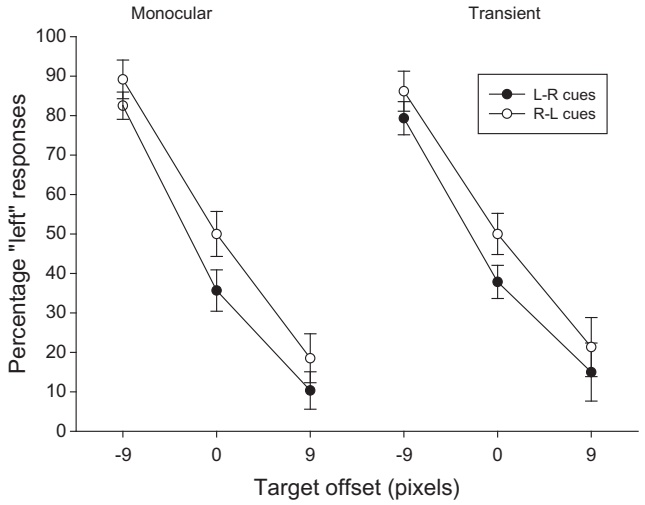

Fig. 4. The mean percentage of 'left' responses for the monocular and transient conditions in Experiment 3. The cues were either top left–bottom right (L–R) or top right–bottom left (R–L). Error bars represent standard error.

tion: −9, 0, 9 pixels) ANOVA. As found before, there was a main effect for target position, $F(2,10) = 82.3$, $p < 0.0001$, as the percentage of left responses decreased as the top Vernier moved from the leftmost target location to the rightmost target location (84.3% at −9, 43.1% at 0, and 16.3% at +9). There was also a main effect for cue, $F(1,5) = 46.6$, $p < .001$, with more left responses for top-right and bottom-left cues. None of the interactions reached significance ($Fs < 2.5$, $ps > 0.12$).

Examining the critical 0° position target position was done with a 2 (condition: monocular vs. transient) × 2 (cue: top-left + bottom right or top-right + bottom-left) ANOVA. While there was no main effect for condition, $F(1,5) < 1$, there was a main effect for cue, $F(1,5) = 17.1$, $p < .01$ (more left responses with top-right cues, 50.4%, than with top-left cues, 36.3%). Importantly, there was no evidence of an interaction between cue and condition ($F(1,5) < 1$), indicating that an ARE occurred in both conditions. Thus, it does not appear that the removal of the ARE in the interocular condition of Experiment 2 was due to the presence of a visual transient.

5. General discussion

The purpose of the present experiment was to gain insight into the ARE mechanism by pinpointing its locus. To accomplish this, we first had subjects undergo both a monocular and a binocular ARE task. In the binocular condition, which replicates previous studies (Pratt & Arnott, 2008; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997), the expected ARE was found. Specifically, brief peripheral cues produced a shift in the perceived location of the Vernier stimulus in a direction opposite to where the peripheral cue was located. In other words, when top-right cues appeared, more 'left' responses were obtained than when top-left cues appeared, even when the two parts of the Vernier were exactly aligned. Importantly, the monocular condition resulted in an ARE that was virtually indistinguishable from the binocular condition, suggesting that the use of only one eye did not compromise the emergence of the ARE. Because having use of both eyes as opposed to one does not give rise to a stronger ARE, it would seem likely that mechanisms exerting their effects in visual areas receiving binocular input do not play a role in the generation of the repulsion effect. Rather, mechanisms with loci in early visual processing where receptive fields are modulated based on monocular information only, seem more plausibly responsible for the observed ARE.

One must take into account the possibility, however, that monocular input sent to high-level visual areas may well activate binocularly tuned cells in a magnitude identical to input from binocular receptive fields. Because of this, the activation of a post-V1 based, binocularly driven mechanism could not initially be ruled out. Experiment 2 included a condition testing for interocular transfer that was incorporated to address the potential ambiguity produced during experiment 1 and to definitively determine whether the ARE can be fully accounted for by a low-level, early visual stream based mechanism. Here, the cue was seen by one eye only, and the opposite eye saw the target only. Results showed that the ARE failed to carry through to the interocular condition, suggesting that information presented to one eye that was necessary for producing an ARE (cue onset) was not combined with information presented to the other eye that was also necessary for producing an ARE (target onset). If the locus of the ARE was in high-level, binocularly governed visual areas, the effect would survive in the interocular condition because crosstalk between the two eyes in receptive fields that process stimuli from both eyes would have integrated the information, leading to an intact repulsion effect. The fact that the effect broke down implies that the ARE results from RF modulation in monocular cells early in visual processing, most likely prior to or in V1 .

How might a mechanism that originates prior to or in V1 give rise to a repulsion effect? In general, visual processing is enriched at the focus of attention (Erikson & Collins, 1969; Erikson & Rohrbaugh, 1970) and RF's are involved in the perceptual enhancement that occurs at the focus (Connor et al., 1994; Desimone et al., 1990; Moran & Desimone, 1985). This focal enhancement incurs a cost to neighboring visual areas, and the ARE may be representative of a loss in RF field coverage in regions adjacent to the attended location which results in a perceived spatial distortion (Suzuki & Cavanagh, 1997). Intriguingly, Suzuki and Cavanagh have proposed a hypothetical model that explains how RF modulation may account for this inaccurate spatial perception. For each 'position-coding' visual unit, a spatial tuning curve can be drawn that corresponds to a specific portion of retinal space. When a stimulus is located at the peak sensitivity of each unit, the strongest response is elicited. In terms of the spatial tuning curve, the peak sensitivity would occur at the apex. So if a Vernier line was presented without a preceding peripheral cue, a 'position-coding' unit governing the appropriate visual space would respond most strongly since the Vernier would be aligned at the apex of the curve – essentially serving as a baseline condition. RF's located beside it would respond less intensely and RF's who's spatial tuning curves do not intersect with the location of the Vernier would not respond at all. If the activity of a given number of units is referred to as the population response and drawn as a population curve, the centroid of this curve would refer to the line that divides the curve into two equal parts. In the absence of a peripheral cue then, the centroid lines up with the perceived location of the Vernier, which is actually the true location of the Vernier. When a brief peripheral cue flashes, however, attention reflexively orients towards it, meaning that one's focus will not entirely be on the Vernier target that is about to appear. Consequently, attention is focused to the periphery and the sensitivity of the surrounding units is depressed, possibly via lateral inhibition. This causes the population response of the group of 'position-coding' units to shift in the opposite direction. Therefore, the centroid now stands off-center with respect to the real position of the Vernier, inducing the observers' errors in localization.

Suzuki and Cavanagh (1997), therefore, argue that the repulsion effect is induced by the orienting of attention to a peripheral location. It is worth noting that they suggest that regardless of whether

this focusing of attention is due to momentary capture by transient cues or due to volitional shifts with central cues, the result is that Vernier targets are repelled away from the attended location. The implication here is that differences between the mechanisms underlying exogenous (“pulled” by peripheral cues) and endogenous (“pushed” by central cues) shifts of attention have no bearing on the emergence of the ARE. In the present study, because only peripheral onset-cues were used, we can confidently infer from the results that the representation of these exogenous cues entered the visual system early (prior to, or in, V1) and that they were processed in a feedforward manner. We can, however, imagine other situations where different types of cues would not be processed in this fashion. When, for example, Suzuki and Cavanagh (1997) induced the ARE by presenting an endogenous cue it is likely that receptive fields in higher cortical areas would have been affected. Voluntary orienting of attention may result in cues entering extrastriate sensory areas via feedback from the frontal cortex (Rosen et al., 1999), and in this case it seems possible that an interocular ARE would survive. Consequently, it is important to consider the possibility that the monocularity of the ARE may be influenced by the type of cue used to attract attention, and this issue should be addressed in future research.

It is worth noting that the conclusion stemming from this study, that the locus of the exogenous cue induced ARE is in early visual processing, is consistent with earlier research from Pratt and Turk-Browne (2003). They found repulsion effects in both perceptual and motor-action tasks, suggesting that the ATR occurred prior to the separation of the ‘object-action’ and ‘object-perception’ pathways. The results of that study, in conjunction with the present findings, strongly suggest that when transient, peripheral cues are used, the ARE is instantiated very early in visual processing.

The ARE offers an excellent tool with which to examine the workings of the human attentional system. Further, since it appears that the effect can originate in low-level visual areas, and can be induced by reflexive shifts of attention, spatial misperceptions may be occurring more or less constantly to us during each day. In essence, the attentional repulsion effect may cause us to misperceive the location of objects in space on a regular basis.

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